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Models of social evolution: can we do better to predict 'who helps whom to achieve what'?

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Models of social evolution and the evolution of helping have been classified in numerous ways. Two categorical differences have, however, escaped attention in the field. Models tend not to justify why they use a particular assumption structure about who helps whom: a large number of authors model peer-to-peer cooperation of essentially identical individuals, probably for reasons of mathematical convenience; others are inspired by particular cooperatively breeding species, and tend to assume unidirectional help where subordinates help a dominant breed more efficiently. Choices regarding what the help achieves (i.e. which life-history trait of the helped individual is improved) are similarly made without much comment: fecundity benefits are much more commonly modelled than survival enhancements, despite evidence that these may interact when the helped individual can perform life-history reallocations (load-lightening and related phenomena). We review our current theoretical understanding of effects revealed when explicitly asking 'who helps whom to achieve what', from models of mutual aid in partnerships to the very few models that explicitly contrast the strength of selection to help enhance another individual's fecundity or survival. As a result of idiosyncratic modelling choices in contemporary literature, including the varying degree to which demographic consequences are made explicit, there is surprisingly little agreement on what types of help are predicted to evolve most easily. We outline promising future directions to fill this gap.

1. Introduction

Apparently altruistic behaviour is the central puzzle that motivates the study of social behaviour. In eusocial insects, workers engage in suicide missions stinging predators to protect their colonies. In cooperative breeding mammals and birds, helpers restrain from breeding to care for the offspring of dominant individuals. Help thus appears to be given at a personal fitness cost to the giving individual, while the receiver improves its fitness. Why such transactions occur was already preoccupying Darwin and, since the revival of the topic through Hamilton's work, a large number of theoreticians and empiricists. Recent years have witnessed a rapid increase in the number of models devoted to this question (table 1).

Why are there so many models? Theoretical work that deals with helping and receiving help can be classified in numerous ways, with, for example, Bergmüller *et al.* [82] classifying the mechanisms based on the presence or the absence of costs to helpers and beneficiaries, how many individuals are involved in the interaction, and whether the interaction has positive or negative effects on the fitness of individuals; Lehmann & Keller [41] dividing the causal routes to cooperation based on the signs of variables such as the probability that an individual interacts again with a partner, the proportion of the benefits generated by a helping act that return to the focal individual, and relatedness; and Hamilton [83] classifying social behaviours based on the fitness effects of the behaviour on the actor and on the recipient.

Table 1. A classification of contemporary models of helping in social animals.

	1.1: help received is an addition to fitness, *w*, or forms elements in payoff matrices	1.2: help received is used to improve fecundity	1.3: help received is used to improve survival	1.4: help received can be used to improve both survival and fecundity
2.1: peer-to-peer cooperation	André [1][a]; Brown & Vincent [2]; Cant [3]; Doebeli *et al.* [4]; El Mouden *et al.* [5][b]; Fletcher & Zwick [6]; Fletcher & Doebeli [7]; Gardner *et al.* [8]; Gardner & West [9,10]; Krupp & Taylor [11][c]; Marshall & Rowe [12]; Mathew & Boyd [13]; Nowak & Roch [14]; Ohtsuki *et al.* [15]; Pacheco *et al.* [16,17]; Perrin & Lehmann [18]; Pfeiffer *et al.* [19]; Rankin & Taborsky [20]; Roberts & Sherratt [21]; Roberts [15,22], [23]; Sherratt & Roberts [24]; Van Cleve & Akcay [25]; Van Dyken *et al.* [26]; West *et al.* [27]	André [1][d]; Alizon & Taylor [28]; Aviles *et al.* [29]; Cant [30]; Day & Taylor [31][e]; El Mouden *et al.* [5][f]; Frank [32][g]; Hamilton & Taborsky [33]; Jansen & van Baalen [34]; Johnstone & Cant [35]; Johnstone *et al.* [36][h]; Killingback & Doebeli [37]; Koella [38]; Kun *et al.* [39]; Le Galliard *et al.* [40]; Lehmann & Keller [41]; Lehmann *et al.* [42][i]; Lehmann *et al.* [43]; Lehmann & Perrin [44]; Lion & Gandon [45]; Mullon & Lehmann [46]; Ohtsuki *et al.* [47]; Panchanathan & Boyd [48]; Rodrigues & Gardner [49]; Rodrigues & Gardner [50]; Teyssèdre *et al.* [51]	Eshel & Shaked [52]	Andras *et al.* [53]; Liao *et al.* [54]; Lion and Gandon [55]; Nowak *et al.* [56]; Smaldino *et al.* [57]; Taylor & Irwin [58]; Taylor [59]
2.2: offspring help their mother	—	Alpedrinha *et al.* [60]; Holman [61]; Lehmann *et al.* [62]; McLeod & Wild [63]; Nonacs [64]; Pen & Weissing [65]; Wild & Koykka [66][j]	Leggett *et al.* [67]	Härdling *et al.* [68]
2.3: subordinates help a dominant (relatedness possible)	—	Cant & Field [69,70][k]; Hamilton & Taborsky [71]; Johnstone [72]; Kokko *et al.* [73]; Reeve & Keller [74][l]; Savage *et al.* [75][m]; Shreeves & Field [76][n]	Shreeves & Field [76][o]	—
2.4: offspring help a sibling	—	Nonacs [77]	—	—
2.5: other asymmetries	Whitlock *et al.* [78]	Cyrus & Lee [79][p]	Rodrigues & Gardner [80]	—

[a]The 'mechanistic model'; the 'main model' belongs to category 1.2.
[b]Their main model.
[c]Offspring interact in a deme and may take differing relatedness into account; probabilities of winning a breeding spot are impacted by B and C.
[d]The 'main model'. The discussion of this paper also recognizes the importance of the possibility that helping might enhance the survival of the recipient, and notes that the consequent demographic effects might be crucially important to enable the initial evolution of helpful tendencies (because only live individuals can reciprocate help); no new model of this effect is provided.
[e]Altruism also impacts survival of the whole group.
[f]Their 'illustrative overview' (extension of their basic model) as well as their 'island model'; their basic model belongs to column 1.1.
[g]Individual behaviour also impacts the survival of the entire colony.
[h]A combination of 2.1 and 2.2 as the authors study two types of help: cofoundress queens help each other, but they also model the spread of alleles dictating the probability that an offspring develops as a worker who will then help its mother to be more productive.
[i]Several effects are included: help (with cost to own fecundity) can increase the survival or productivity of the entire deme, as well as the survival of juveniles (which can be thought to be equivalent to increasing neighbour's fecundity; all adults die after reproduction).
[j]The mother is the female function of a hermaphrodite.
[k]Subordinates (with symmetrical relatedness to dominant breeder) form a queue to help a single dominant breeder, who then has higher fecundity.
[l]A very large number of models in reproductive skew theory also use this assumption (help is modelled rather indirectly in this field as a decision to stay that has fixed helpful consequences, which is why we do not list many examples in table 1). In this field, the most detailed examination of the consequences of variation in the 'who helps whom' question is Reeve & Keller [81], who consider a dominant–subordinate relationship and examine the consequences of potentially asymmetric relatedness of each individual to the offspring produced by the other individual. Asymmetries can be important, for example, when contrasting mother–daughter versus sibling associations.
[m]Savage *et al.* [22] include a demographic response where a helped mother can produce more young. However, life-history details such as survival from one year to the next are abstracted away.
[n]Here help is not evolving but the decision to stay is. The productivity of the dominant breeder is assumed to improve with group size (model 1) or the probability of complete failure is decreasing with group size (model 2—insurance). Their model 3 belongs to category 2.3.
[o]Help is not evolving (the decision to stay is), but the article is noteworthy for making the point (model 3) that the helper's fitness can decrease if the dominant lives longer, given that the helper might inherit the dominant status if she outlives the dominant and all other 'queuers'.
[p]Modelled explicitly as increased survival of children; help can flow in principle in many directions between three age-groups, assuming trade-off structures that are relevant to humans.

It appears to be a less popular exercise to ask two questions that appear of equally fundamental importance to us: (i) who helps whom, and (ii) what does the recipient achieve with the help it received—more precisely, which life-history trait of the helped individual is improved? In nature, helping often shows unidirectional 'flow' from one individual to another, at least when viewed over suitably short timescales. The examples of insects and vertebrates above each had a beneficiary, for whom the interaction is clearly desirable, and an individual whose behaviour is harder to explain. The 'choices' made by the latter individual, often called 'helper' or 'subordinate', prompt the study of social behaviour in the first place. The unidirectionality of the flow does not necessarily last forever: in studies of reciprocity, for example, the roles of helpers and recipients of help can switch within seconds. More generally, a whole lifetime perspective, including potential reversals of help directionality, can be important to understand the helper behaviour early in life, as the benefits of past helping decisions may only materialize later (e.g. [73,84]).

Once we realize that a helper cannot necessarily fully control what the beneficiary achieves with the help received, this begs a further question: how does the beneficiary's behaviour impact the inclusive fitness of the helper? To put this abstract statement on a concrete footing, consider a young individual who benefits from staying in its natal territory because of the prospects of inheriting it later. While waiting, it may behave as a helper, perhaps because this leads to inclusive fitness if the fecundity of a related dominant breeder is elevated, or because helping the dominant is required to avoid eviction (the 'pay-to-stay' hypothesis, [85,86]). Now consider what happens if the dominant uses some of the help received to prolong its own lifespan. This does not necessarily require direct life-saving actions by the helper, of the type of Haldane's thought experiments involving saving relatives from drowning. Helpers feeding the dominant's young in the nest may simply enable the dominant to work less hard, which then can allow energetic reallocation towards self-maintenance or fewer risks taken during foraging. Either way, the dominant lives longer as a result of *load-lightening* (documented e.g. in red-cockaded woodpeckers [87], fairy-wrens [88,89] and long-tailed tits [90]).

Load-lightening can clarify otherwise puzzling cases where helping does not seem to have straightforward effects on breeding success. From the helper's perspective, however, load-lightening can be problematic. Although load-lightening was initially proposed to improve the inclusive fitness of the helper as a result of increased lifespan of related breeders [81], this should be weighed against the negative effects of reduced territorial inheritance prospects if many helpers die before they ever inherit.

As a net effect, it may be costly for a helper to prolong the recipient's lifespan [76].

However, helping can also evolve specifically to keep a partner alive. Consider the concept of *partnership*, *sensu* Eshel & Shaked [52], where individuals are called partners when it is in their best interest to help each other, if by doing so they increase the probability of being together in the future when, for similar reasons, they will continue to help. Reduced mortality offers the simplest way for this probability to be elevated: put simply, it is very difficult to behave reciprocally if one is dead. Partnership thus takes elements of reciprocity theory but emphasizes the life-history context. Similar thoughts have been developed, with subtly varying terminology, by Roberts [22], Garay [91], Port & Cant [92] and Smaldino *et al.* [57] (see also [93,94]).

The ideas of load-lightening on the one hand, and partnership (and its variants) on the other, differ not only in what the beneficiary's longer life means for the fitness of the helper. These sets of literature also differ in how they treat one of our central questions: who helps whom. Load-lightening is typically assumed to involve pre-existing asymmetries, with a breeder being helped by non-breeding subordinates (usually family members, see [68,75] for theory, and [88–90] for empirical results). Ideas involving partnership, on the other hand, are usually developed using peer-to-peer cooperation, a term that we use for interactions with no defined asymmetries between the interacting individuals (table 1).

Here we point out that most theoretical literature on cooperation treats our two questions (who helps whom, and what is achieved with the help received) as given—but, intriguingly, the type of structural model assumptions differs starkly between subfields. These differences probably arise because students of social evolution emphasize either mathematical convenience or specific insights about the natural history of one or several species. There is very little integrative work in that area, and we will produce one step towards such modelling. More generally, we will highlight how drawing links between model assumptions could prove useful in future work.

2. Who helps whom, and what is achieved with the help received: what are researchers assuming?

We begin by investigating a large sample of current theoretical models addressing the evolution of helping (table 1), which we have classified according to 'who helps whom' and also what the help is assumed to achieve (i.e. which life-history traits of the helped individual are improved). We do not intend our list of studies to be comprehensive in the sense of covering all existing models of cooperation or helping; thus we did not use systematic literature searching techniques that are used in meta-analyses. We instead aim to provide a relatively comprehensive overview of the current diversity of modelling assumptions, and to achieve this, we favoured including models from a large number of currently active researchers over presenting all variants on a given topic from a particular research group. This approach should give a better view of the diversity of assumptions present in contemporary literature on models of the adaptive evolution of helping, given that two different research groups are more likely to differ in the assumption structure of their models than two papers from the same research group.

Based on the large number of models we include, we are quite confident of providing readers with a relatively accurate picture of common versus rare modelling assumptions. For example, while we do not cover models concerning the production of public goods, a random sample of public goods models is probably sufficient to convince an interested reader that they as a rule study interactions among peers (i.e. repeat the pattern of table 1). Note that we also excluded studies that did not consider helping to be an evolving trait. For example, Wild [95] models a scenario where offspring helping a parent can make the parent survive better,

but this is not a model of the evolution of helping but of sex ratio evolution.

We classified models into 5 × 4 categories according to (1) 'who helps whom', and (2) what the help achieves for the recipient of help. For question 1, we used the term peer-to-peer cooperation if the model includes no inherent asymmetry between the interacting individuals (1.1). The other possible categories are (1.2) offspring helping their mother, (1.3) a more general category of subordinates helping a dominant, (1.4) offspring helping a sibling and (1.5) 'other asymmetries'. In practice, this last category only includes three models: one where individuals share resources reciprocally but differ in the shape of the function relating resources to fitness [78], one where reproductive values and abilities of individuals can differ [80], and an examination of age-dependent helping in a stylized human life history [79]. Among the more commonly occurring assumption structures, models in category 1.3 are also often interpretable as mother–offspring associations (they often have a relatedness term which can be set to e.g. $r = 0.5$), but we have kept them separate from 1.2 whenever they also offer more flexible interpretations.

Question 2 likewise has categories with somewhat fluid boundaries. We used the following classes: (2.1) help received is used to increment fitness in an abstract way (usually this involves notation where received help manifests itself as an additive increase in fitness w, or as a benefit term b or B in a payoff matrix), (2.2) the recipient's fecundity is increased, (2.3) the recipient's survival is improved or (2.4) the model considers explicitly that the recipient may improve either survival or fecundity. The boundaries are fluid with respect to (2.1) and (2.2), because abstract models of fitness—category 2.1—are easiest to interpret if gene frequency changes are assumed to follow from fecundity differences and generations are discrete (category 2.2). Therefore, in our classification, the decision to place a model in category 2.1 or 2.2 was more strongly dependent on the language used to describe the model rather than its mathematical structure *per se*. If instead of abstract 'fitness' or 'payoffs' the description of the model explicitly refers to offspring production or the fecundity of the parent, then we considered 2.2 to be the appropriate category.

While the placement between (1.2)–(1.3) and (2.1)–(2.2) can remain mildly subjective, this does not have an impact on the conclusion that is immediately apparent from examining table 1: the vast majority of models assume peer-to-peer cooperation (1.1), and likewise the vast majority of them either do not specify the effects of help beyond an abstract improvement of fitness (2.1) or they force the recipient to be more productive with no effect on the recipient's survival (2.2). Another relatively populous group of models has a mother–offspring or a more general dominant–subordinate structure; these models assume that the dominant breeder's productivity (fecundity) is improved by the help received. Other types of models are rare.

It therefore appears that model development follows one of two possible routes. In the first route, researchers have taken to heart the recommendation that useful models must simplify the world to be able to produce tractable results on questions of interest ([96,97]; for discussion of this, specifically in eco-evolutionary contexts, see [98,99]). Thus, when constructing a proof-of-principle of a particular causal route to cooperation, e.g. by focusing on the prospects that indirect reciprocity (or punishment) maintains cooperation, the interacting organisms' identity and life history are kept as simple as possible. Specifying no particular asymmetries between the interacting organisms then leads to assumption (1.1), and avoiding spelling out any life-history detail leads to assumption (2.1) or (2.2).

The second route is to produce models that take some of their assumptions from what we know about the natural history of social animals. While researchers vary in how widespread they consider cooperative interactions of the peer-to-peer type (this debate is its liveliest in the context of reciprocity, e.g. [1,100–102]), there is little doubt that cooperative interactions very commonly involve related individuals. Whenever a modeller is drawing inspiration from systems that relate to family living, it is consequently commonplace to take the family structure as a given. This tends to make assumptions about helping unidirectional: the subordinate either helps the dominant or fails to do so; other directions for the flow of help are not permitted.

Do the above patterns reflect an unsatisfactory state of affairs? One could argue that 'it depends'. Each of the above reasons to end up with a certain model structure is, by itself, legitimate. However, it also remains the case that models, when used as thinking tools, guide our efforts towards those aspects of a problem that a model considers, and away from those that are taken as given. Table 1 therefore yields three insights. First, theoreticians rarely write justifications for the structural choices made regarding 'who helps whom' and 'what does help achieve', despite different models making clearly different choices (table 1). Second, little theory development appears to happen in 16 out of the 20 squares of table 1. Third, working out how the evolutionary logic of a specific process might alter its character across several different options in table 1 appears to be a particularly unpopular activity.

3. What do we already know about the underexplored parts of table 1?

(a) The first question: who helps whom?

Theoreticians are not in the habit of making models flexible enough to consider variations in the direction in which help flows. Whitlock *et al.* [78] and Rodrigues & Gardner [80] are two rare exceptions. Rodrigues & Gardner [80] highlighted the importance of asymmetries in individual quality, including reproductive value and the ability of engaging in social interactions (termed social value), for the evolution of helping and harming. They studied cases in which group members could adjust their behaviour according to their own and the recipients' quality, concluding that in viscous populations low-reproductive value individuals would engage in extreme altruistic behaviour if their behaviour could be directed towards high-reproductive value individuals, but this is replaced by extreme harming behaviour if their behaviour is directed towards low-reproductive value individuals.

Whitlock *et al.* [78] extended reciprocity theory to asymmetries in the costs and benefits of donors and receivers in the context of reciprocal resource sharing. They concluded that if one individual is consistently in a 'needier' state than the other (in the sense of resources gained having the potential to greatly impact its future success), then kin selection is required for one individual to keep helping the other. Truly reciprocal sharing among unrelated adults, by contrast, is rare, as under these conditions temporally stable variations

in individual state do not select for helping. Rapid frequent switches in state can, however, stabilize such interactions (vampire bats that sometimes fail to feed are the classic e.g. [103]).

Do the results [78] give a justification for the preponderance of models where parental fecundity is increased when helpers help? The answer is a qualified yes, in the sense that such models are consistent with helper behaviour that involves resources (usually food) given directly to offspring, which the modeller then chooses to quantify as an increase in their parent's fecundity [104]. Feeding the young also ranks among the most common types of help given in animal societies—though such a statement has to be qualified by a reminder that the diversity of tasks performed is immense, with just a few examples being the 'babysitting' of young meerkats [105]; colony defence in social insects [106,107] with the extreme example of self-sacrificing *Forelius pusillus* ants sealing off the nest entrance from outside (a suicidal activity as the workers completing the job will die overnight, [108]); participation in territorial boundary disputes [85,109]; and honeybee swarms searching collectively for new nest locations [110]. All of these activities enhance the performance of the colony or group one way or another, but only some of them are directly interpretable as increases in a dominant breeders' fecundity.

We are unaware of a single theoretical study that aims to derive general expectations in the direction of help given, when the direction is a flexible trait. Empirically, ontogenetic task switching is well studied, e.g. in honeybees [111] and ants [112]. In humans, across-generation energy flows have been quantified empirically [113–115] as well as modelled [79]. As foreshadowed by Rodrigues & Gardner [80], there appears to be scope to develop general—i.e. not species-specific—life-history predictions where reproductive values and skill levels change during ontogeny, with the speed of changes being impacted by upstream or downstream flows of helping between generations.

(b) The second question: what is achieved with the help?

Why do modellers far more often assume that help increases the recipient's fecundity than her survival? Below we discuss two reasons, one perhaps more strongly applying to those models that imagine the simplest possible world in which to study a phenomenon, the other to the more strongly natural-history inspired ones.

The first reason is mathematical convenience. In most models generations follow each other in discrete time, either explicitly or implicitly. This is not necessarily a result of any particularly high frequency of non-overlapping generations in the real world: iteroparity is the norm, e.g. in cooperative breeders. However, discrete generations are mathematically more convenient as they allow a neat alternation of fitness calculations and consequent gene frequency change from one generation to the next. The popularity of fecundity over survival effects then arises because once one has made the assumption of generations being discrete, it tends to be more convenient to assume that individuals have fixed survival up to their single breeding season and then fecundity varies, than to assume variable survival followed by identical fecundity of survivors. Some models offer hybrid approaches, such as Rodrigues & Gardner's [80] where survival to a single breeding event depends on social interactions while fecundity depends on individual quality.

Rather interestingly, some models with overlapping generations use mathematical convenience as a reason to model survival benefits (in contrast to many discrete-generation models in which convenience leads to fecundity benefits being modelled). With overlapping generations, this convenience argument can arise in the following way. Leggett *et al.* [67] model a setting where a long-lived breeder can produce clutches sequentially. Their choice to model fecundity benefits is justified by the wish to avoid dealing with a complicated cascade where accumulating numbers of helpers feedback to more offspring being produced, who in return may provide help and so on. While a similar accumulation process could happen through different-aged offspring accumulating in a territory as helpers, this is not permitted to happen in Leggett *et al.* [67] as offspring are assumed to die unless they successfully compete for a breeding vacancy after one round of helping.

A second potential reason for the relative scarcity of models that include survival effects is that nature might provide us with far more examples of help that increases the recipient's fecundity than her lifespan. We are not sure there is good enough data to evaluate this claim quantitatively, given that fecundity effects can be documented much more quickly than measuring entire lifespans. However, if true, there remains the interesting question of how and why such an asymmetry arose in nature. We suspect that part of the reason is simple: offspring are the needy ones in the sense that an investment in their well-being can bring out the best 'bang for the buck', while adults are more capable of surviving without others' help (see [79]). If we have made the choice to assign their survival increases as parental fitness, then parental fecundity is increased based on an efficiency argument.

Even if modelling choices are sometimes made for the sake of convenience, they might therefore not be too far off from reality. However, a series of models, which we will discuss in the next section, shows that we should not ignore the interesting possibility that cooperative systems are significantly impacted by lifespan effects.

(c) Not all researchers have ignored the possibility that lifespan can be altered by help

So far, the efforts spent in understanding effects of help on lifespan appear to form a rather scattered research programme. The relevant models listed in table 1 yield the following summary.

In Andras *et al.* [53], agents interact in repeated rounds of Prisoner's Dilemma games and accrue resources, which they also continually spend on living costs. If resources fall below a threshold, the organism dies; if the organism lives past a certain age, it reproduces, and fecundity now depends on accumulated resources. Smaldino *et al.* [57] use a similar approach, but now agents reproduce as soon as their resource levels exceed a certain threshold and there is also a site available to host the offspring. The questions addressed by these studies revolve around whether harsh environments, variously defined as difficult or unpredictable resource acquisition, select for cooperation. This is quite a different goal from investigations of the effects of promiscuity on helping behaviour (the aim of Leggett *et al.* [67] already mentioned above) or how variation in individual quality mediates the evolution of unconditional and conditional social traits (the aim of Rodrigues & Gardner [80], also mentioned above).

The above papers are not primarily targeting survival effects as an object of study, despite such effects happening to be part of the model structure. Similarly, fecundity and survival effects are part of recent models that are primarily designed to examine arguments in favour or against kin selection as an explanatory tool [54,56]: their mathematical treatment includes two types of consequences of a worker's decision to stay in the colony, and both birth and death rates can depend on colony size. However, these models (and the debates surrounding them) have not focused on exploring the consequences of these effects.

(d) There are some explicit examinations of survival effects

Far more interestingly for the current review, some models explicitly invite the reader to think about the intricacies of survival as a trait that reacts to help received. Shreeves & Field [76] quantify, in one of their models, the negative consequences of a dominant breeder's lifespan improvements for the prospects that the helper ever inherits the dominant position. Other modellers have taken an approach where help that increases fecundity is explicitly contrasted with help that increases survival [55,58]. Taylor & Irwin [58] also comment on the fact that non-zero survival from one breeding season to the next increases relatedness within a patch, which has a direct help-promoting effect even if the high survival is not a result of helpful actions. Lion & Gandon [55], in turn, show the validity of this argument to be limited, given that high survival can also create environments where competition for breeding sites is fierce. Ideas of 'partnership' [52] follow a different line of thinking. In the model of Eshel & Shaked [52], there is no relatedness nor is there fecundity: individuals (who are peers of each other) are simply assumed to benefit from helping each other because of reciprocal increases in each other's lifespan—think of an arctic expedition which is easier to survive in a small group than alone.

An interesting feature of the partnership model is that helpers whose partner dies are assumed to spend some time alone—and vulnerable (in terms of a higher mortality risk per unit time)—before being joined by another partner. If finding partners is easy, then levels of cooperation fall [52]: put bluntly, there is not much point in keeping a team mate alive, if a new one appears as soon as the previous one dies. This leads to a feedback where the effort spent to keep others alive can drop further precisely because it is no longer important to keep only moderately helpful partners alive and well (the relative benefit of being in a team, compared with being alone, having already decreased).

The development of models that explicitly contrast fecundity benefits and survival benefits [55,58] has progressed completely independently of these ideas of partnership. In Taylor & Irwin [58], individuals live in patches of N breeders from which some offspring disperse (probability d) and die en route with probability k. They assume weak selection based on fecundity or survival benefits b, at a cost c to the helper which can be written as impacting either survival or fecundity. The model shows that in a structured population with kin interactions, it is harder to select for help that improves the recipient's survival than if her fecundity is improved; however, the difference becomes milder—and helping becomes in general more likely—if survival is high as a whole.

The reason why it might be beneficial to help someone survive differs between Taylor & Irwin's [58] model and partnership models. The former structured-population model assumes weak selection, such that the model tracks small changes in the prospects of producing (related) offspring, either because the parent was more likely to survive, or because it was more fecund as a result of help. To some extent, weak selection is an approximation that allows us to ignore more complex secondary effects such as increasingly prolonged mutualistic interactions between specific individuals, i.e. the possibility that partnership ideas [52] focus on. Indeed, in Taylor & Irwin's model [58], patches were always at carrying capacity (N), prohibiting any causalities of the Eshel-Shaked type from operating where it is riskier to live alone than paired with a helpful partner.

In Taylor & Irwin's model [58], it does not matter whether costs of helping are paid in units of survival or fecundity. This conclusion changes if one chooses to track the consequences of helping on demography (population density changes). Lion & Gandon [55] took a new look at the problem of helping to improve others' fecundity or survival and included feedbacks between behaviour and population dynamics, thus no longer assuming that all sites are at carrying capacity. In their overlapping generations model, a site does not have N breeders like in Taylor & Irwin's world; instead, it can be empty or have one individual residing in it. Individuals are connected to n other sites, which offer settlement prospects for offspring if they are empty. Helping between neighbours improves either the fecundity or the survival of the recipient, and decreases either the fecundity or the survival of the helper. The model then proceeds to describe the birth–death process, where mortalities and fecundities are modelled as rates (continuous time).

(e) . . .Yet current conclusions are all over the place

The conclusions of Lion & Gandon [55] differ quite dramatically from Taylor & Irwin [58]: if helping improves a neighbour's survival, it tends to evolve much more easily than if it improves her fecundity (except when habitat saturation is high, in which case the predictions of the two models become similar). Also, high survival *per se* does not promote helping in Lion & Gandon's model [55]—rather the opposite. This is because high survival leads to strongly saturated habitats, and it is not useful to help a neighbour when offspring lack future prospects unless there are empty sites (an assumption in Lion & Gandon [55]).

Taylor [59], in turn, shows—again using a continuous-time model—that the answer to which life-history improvement is better at creating conditions favourable for the spread of altruism can depend on a 'demographic protocol': if offspring replace adults in the sense that an offspring being born increases the mortality of adults (offspring cause adults to die), then help that improves the recipient's survival is more easily favoured than fecundity-boosting help. If, on the other hand, deaths of adults create space that allows offspring to thrive, the opposite prediction arises.

The way each model differs in more than one aspect of its assumption structure makes it rather hard to state which differences are truly responsible for the differences in insight. Note, for instance, that Lion & Gandon's [55] differs from how the relationship of habitat saturation, survival and cooperation has been treated in the literature on social evolution, where an oft-stated prediction is that habitat saturation improves prospects for sociality when the helping

decision first requires a decision to stay at home [40,116–118]. Models may also highlight nuances and caveats: for example, increasing survival of breeders can have a fundamentally different effect on the prospects of stay-at-home helpers from increasing the survival of dispersers, even if both increase habitat saturation ([119]; see [45] for another set of complexities). All this prevents us from saying much more about the state of the present theory than that unless we learn to look at predictions based on survival too, we risk staying in a situation where idiosyncratic choices for life histories of modelled organisms make it quite hard to see the forest for the trees.

4. How factors could interact: a simple model

Here we develop a simple model that is not a complete overview of all factors, but a step towards looking at survival and fecundity effects when the group dynamics is explicitly modelled. We consider different kinds of social behaviour depending on 'who helps whom'. We consider behaviours that entail trade-offs *between* breeders, in which breeders trade-off their own fecundity or survival for the fecundity or survival of their partners, but there are also trade-offs *within* breeders, in which breeders trade-off their own fecundity for their own survival.

Our model assumes that breeders can either live solitarily or in a group with one partner. The survival and fecundity of solitary- and group-living breeders may differ. Each season, solitary breeders give birth to f_1 offspring, and survive until the next breeding season with probability s_1. Group living breeders give birth to f_2 offspring, and survive until the next breeding season with probability s_2. After being born, offspring become either solitary breeders with probability $1-g$, or group-living breeders with probability g. Solitary breeders may form new partnerships if they find another solitary breeder, which occurs with probability a, otherwise with probability $1-a$ they remain solitary. Group-living breeders become solitary breeders if their partners die, but the partnership remains intact if both breeders survive.

Our aim is to understand how selection acts on the social behaviour of group-living breeders, and to contrast the selection pressures acting on fecundity and on survival. We take the neighbour-modulated approach to kin selection to derive the selection gradients acting on social behaviour ([120–122], see the electronic supplementary material, appendix A for details) that mediates the fecundity and/or the survival of group members. A slight increase in the expression of these behaviours causes a cost (denoted by C) or benefit (denoted by B) to breeders [80]. We first ask whether a behaviour that entails a fecundity-cost to the actor and a fecundity-benefit to the partner is favoured by natural selection; this happens if

$$-C+Br>0, \tag{4.1}$$

where r is the relatedness between partners. The above inequality shows that relatedness is here crucial. The actor has C fewer offspring, and the actor's partner has B additional offspring, each with a value r to the actor.

Let us now consider a behaviour that has a survival-cost to the actor and a survival-benefit to the partner. We find that natural selection favours this behaviour if

$$-CV_2+Bs_2(v_2-v_1)+BrV_2-Crs_2(v_2-v_1)>0. \tag{4.2}$$

The first term of this inequality describes the cost to the actor in terms of her expected reproductive value (denoted by V_2). The expected reproductive value of a breeder living in a group is v_1 if the partner dies, which occurs with probability $1-s_2$, and is v_2 if the partner survives, which occurs with probability s_2. Hence, $V_2=(1-s_2)v_1+s_2v_2$. The second term describes the benefit to the actor of a slight increase B in the survival of her partner. The third term describes the indirect fitness gain to the actor of a slight increase B in the survival of her partner. Finally, the fourth term describes the inclusive fitness cost to the actor. As the actor is less likely to survive, it is more likely that the partner will become a solitary breeder, which leads to the concomitant decrease in the partner's reproductive value (i.e. v_2-v_1).

Let us turn the attention to cases in which a behaviour entails a survival-cost to the actor and a fecundity-benefit to her partner. The condition for the evolution of such behaviour is given by

$$-CV_2+BrV_o-Crs_2(v_2-v_1)>0. \tag{4.3}$$

The first term represents the survival cost to the actor, whose reproductive value is V_2. The second term represents the additional offspring, whose reproductive value is V_o and relatedness is r, gained by the actor's group mate. Finally, the third term represents an inclusive fitness cost to the actor: as the actor is less likely to survive owing to the expression of the social behaviour, the group mate is more likely to become a solitary breeder, with a concomitant decrease in the partner's reproductive value.

We now ask whether a behaviour that entails a fecundity-cost to the actor and a survival-benefit to her partner is favoured by natural selection. The condition for the evolution of such social behaviour is given by

$$-CV_o+Bs_2(v_2-v_1)+BrV_2>0. \tag{4.4}$$

The first term of this inequality describes the loss to the actor, who has C fewer offspring, whose expected reproductive value is V_o. The expected reproductive value of an offspring is v_1 if the offspring breeds alone, which occurs with probability $(1-g)$, and v_2 if the offspring breeds in a group, which occurs with probability g. Hence, $V_o=(1-g)v_1+gv_2$. While sacrificing her fecundity, the focal breeder increases the chances that her partner survives by a factor B. As the partner is more likely to survive, the focal actor is more likely to breed in a group, rather than alone, and therefore there is an increase in her reproductive value (i.e. v_2-v_1), assuming that the focal actor survives (probability s_2). Finally, there is an indirect fitness benefit to the actor. The indirect fitness benefit is discounted by the relatedness between the actor and her partner, and it depends on the expected reproductive value of a group-living breeder (V_2).

Up to now we have considered trade-offs, either in terms of fecundity or survival, between different breeders. We now consider a trade-off within breeders. We ask whether a breeder is favoured to extend her longevity at a cost to her fecundity, i.e. we ask if a decreasing reproductive effort is favoured. The condition for the evolution of a slightly lower reproductive effort is given by

$$-CV_o+BV_2+Brs_2(v_2-v_1)>0. \tag{4.5}$$

The first term describes the cost to the focal breeder, who has fewer offspring, whose value is $V_o=(1-g)v_1+gv_2$. The second term describes the benefit to the focal breeder. Finally,

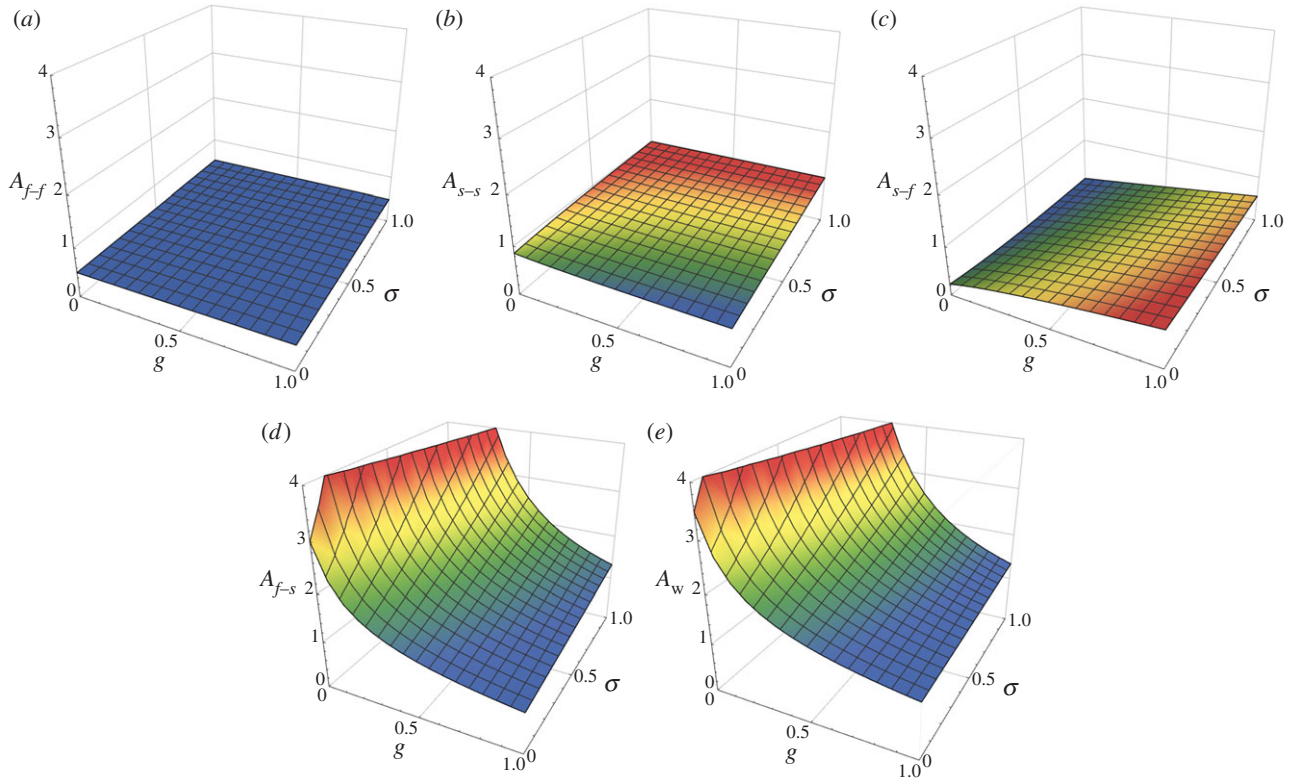

Figure 1. The potential for helping (or for investment into survival) (A) as a function of an offspring's probability of joining a group (g) and as a function of the reproductive inequality between solitary- and group-living breeders (σ), for cases in which: (*a*) a mother gives up some of her fecundity to increase the fecundity of her partner; (*b*) a mother gives up some of her survival to increase the survival of her partner; (*c*) a mother gives up some of her survival to increase the fecundity of her group partner; (*d*) a mother gives up some of her fecundity to increase the survival of her partner; (*e*) a mother gives up some of her fecundity to increase her own survival. Parameter values: $a = 0.5$; $r = 0.5$; $s_1 = 0.1$; $s_2 = 0.9$. (Online version in colour.)

the third term describes the indirect fitness benefit to the focal breeder owing to an increase in the reproductive value of the focal breeder's partner.

Setting the l.h.s. of inequalities (4.1)–(4.5) to zero, and rearranging the resulting equations, we get an identity of the form $C/B = A$, in which A is the potential for helping. This is the highest cost-to-benefit ratio of a behaviour that is still favoured by natural selection. If the potential for helping is positive ($A > 0$), then selection favours helping (for which $B > 0$), while if $A < 0$, then selection favours harming behaviours (for which $B < 0$) [80]. In the context of trade-offs within breeders, A describes the potential for investment into survival (or disinvestment into reproductive effort), which we denote by A_w.

In figure 1 (see also the additional figures in the electronic supplementary material), we graph the potential for helping against parameter values. Without loss of generality, we set the fecundity of group-living breeders to one (i.e. $f_2 = 1$), and the fecundity of solitary breeders to $1 - \sigma$, with $0 \leq \sigma < 1$, such that σ can be interpreted as the reproductive inequality between solitary and group-living breeders.

As shown in figure 1*a*, under a between-breeders fecundity–fecundity trade-off neither the likelihood that an offspring finds a partner (g) nor the reproductive inequality (σ) plays a role in the evolution of helping. Group mates simply exchange their own offspring for the offspring of their partners, and relatedness to offspring is the key factor mediating such transactions (see inequality (4.1)). Let us now focus on a between-breeders survival–survival trade-off, as shown in figure 1*b*. The potential for helping rises when an offspring's probability of finding a partner falls, but also when the reproductive inequality rises. This is because both factors increase the benefits of living in a group (v_2) relative to that of solitary breeders (v_1). When the fecundity of solitary breeders is extremely low (high σ), their reproductive value becomes negligible (i.e. $v_2 - v_1 \approx v_2$), at which point all costs and benefits in inequality (4.2) depend only on the reproductive value of group-living breeders. As a result the potential for helping becomes insensitive to the probability that an offspring finds a partner (g).

Let us now contrast a survival–fecundity trade-off (figure 1*c*) with a fecundity–survival trade-off (figure 1*d*). Figure 1*d* shows that, under a fecundity–survival trade-off, the potential for helping rises when an offspring's probability of finding a partner falls, but also when the reproductive inequality rises. This is because if an offspring can easily find a partner (high g), their relative value increases, and therefore there is less incentive for a breeder to invest into a partner's survival at a cost to her own fecundity. When it is easy for offspring to find partners (high g), the reproductive value of offspring is reduced to v_2 ($V_o = v_2$), and therefore the potential for helping becomes less sensitive to the fecundity of solitary breeders. We also find that the potential for helping rises when reproductive inequality rises. This is because while group-living breeders enjoy higher fecundity, offspring may become solitary breeders who enjoy lower fecundity, and therefore their expected reproductive value (i.e. V_o) is relatively lower than that of group-living breeders (i.e. V_2). Perhaps not surprisingly, the potential for helping under a survival–fecundity trade-off contrasts with the potential for helping under a fecundity–survival trade-off (cf. figure 1*c*,*d*).

Finally, we consider a within-individual fecundity–survival trade-off (figure 1*e*). We find that in this case the

potential for investment into survival (or disinvestment into reproductive effort) follows a qualitative pattern that is similar to the potential for helping (cf. figure 1*d*,*e*). However, they are not exactly identical. This is because in the potential for helping scenario (i.e. between-individual trade-off) a breeder's investment into the partner's survival has a secondary effect on the helper's survival, while in the potential for investment into survival (i.e. within-individual trade-off) scenario a breeder's investment into her own survival has a secondary effect on the partner's survival (compare inequality (4.4) with inequality (4.5)). This discrepancy shows that a focal breeder and her partner may disagree over the value of the focal breeder's survival, which suggests a conflict of interests among group members over life-history traits.

How does our model compare with previous models? Taylor & Irwin [58] and Lion & Gandon [55], for example, assumed an unchanged number of breeders in each patch, with no link between social behaviour and the size of a group. This contrasts with our model, in which the social behaviour of an individual influences the dynamics of groups. The contrast between our model and that of Eshel & Shaked [52], in turn, is that Eshel & Shaked [52] did not explore different kinds of trade-offs between fitness components (fecundity versus survival). Our model, in turn, has not incorporated various features that are included in other models, and in general there is much scope for further work. For example, we have assumed that the probability of finding partners (i.e. g and a) are fixed parameters; future work could make these parameters depend on the number of solitary breeders in the population and on the saturation of the environment (e.g. [55]). We have also assumed that offspring do not remain with their mothers as adults. Instead, one could consider that offspring may remain in their natal group, which can influence their future payoffs as well as that of their partners (e.g. [73]).

5. And wait, there is more! Load-lightening and allied phenomena

Above, we expressed surprise regarding the scarcity and idiosyncratic nature of models that have ever contrasted effects of survival improvements with those of fecundity improvements. It appears that an even smaller section of the vast literature on cooperation considers conflict between helpers and recipients of help because the latter might allocate the benefits in a way that is not necessarily ideal from the helper's perspective.

Load-lightening, for instance, frees resources for beneficiaries, who can then reallocate to other fitness components, such as increasing the current number of young produced [75] or surviving to the next breeding attempt [68]. But load-lightening in the context of alloparental care is not the only type of life-history response of beneficiaries that can alter the payoff and conflict structure of a cooperative interaction. Consider, again, the mental image evoked by the study of Eshel & Shaked [52]: arctic explorers helping each other survive. Under some conditions, it might be the best option for one of the explorers to use some of the resources (e.g. shared food) to increase her own current reproductive effort; it is easy to see why in the context of partnership such an action is not at all in the interest of the unrelated partner, when mutual survival promotion was the reason behind cooperation—except if the juveniles grow up and quickly become helpful themselves [73]. This highlights the interesting point that types of help can differ greatly in how easy it is for the helper to keep the help within the 'intended' use. Saving someone from drowning has direct effects on lifespan, but sharing food (even in the form of directly feeding someone's young) can have a multitude of consequences. Adaptive shifts in the recipient's life history might sometimes jeopardize the stability of cooperation.

6. Conclusion: what to do?

It would be tempting to finish a review paper of current modelling efforts in a field by presenting a model that ties all loose ends and provides the ultimate overview. However, we believe we have highlighted somewhat too many loose ends for them all to be solvable in one go; our model, for instance, could be classified as category (1.4)–(2.1) of table 1 instead of spanning all of them. Instead, we end by making a few recommendations for future work.

First, it would be highly useful if, when developing theory, researchers paused for a moment to justify the placement of their model structure in the categories of table 1. The undercurrents that we suspect to underlie researchers' preferences are perhaps best thought of as necessary evils. Mathematical convenience is not laziness (it can mean tractability), and taxon-specific assumptions can make sense. However, if the choices are never explicitly justified, a particular structural choice may guide our thinking in ways that remain unexamined and unchallenged.

Second, it would be desirable to examine how conclusions change if the recipient of help was not constrained to use the help in one particular way. Increases in fecundity differ in their demographic consequences from increasing one recipient's survival. The number of new individuals competing for local resources can potentially become much higher when current fecundity is increased, but we hesitate to state that the effects on demography are strongest with fecundity effects in general: depending on the system, adults helping each other might create such substantial lifespan improvements that could lead to particularly slow turnover in demographic processes. All this remains underexplored.

Third, our current theoretical understanding of 'who helps whom' is poor. The fact that offspring are the recipient of help (which then is modelled as a fecundity-benefit for the parent) is probably based on nonlinearities in fitness curves of the type presented by Whitlock *et al.* [78], or based on asymmetries in reproductive value and social value of the type presented in Rodrigues & Gardner [80]. But as the curves, reproductive value, and social value change with age, and effects of help in general are not invariant with respect to time if a social group experiences demographic changes [32], it appears that the field could very usefully work towards integrating ontogenetically determined asymmetries with analyses of selection to improve a partner's fecundity or survival. We therefore hope that conclusions will not be 'all over the place' long into the future.

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